



Effects of light during early larval development of some aquacultured teleosts: A review

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ABSTRACT

Light is a key environmental factor that synchronizes all life-stages of fish, from embryo development to sexual maturation. The underwater photo-environment is complex since light characteristics (i.e. intensity, photoperiod and spectrum) depend on the absorbance properties of the water column. The aim of this paper is to review the effects of artificial lighting conditions on the performance, development and welfare of some fish larvae of commercial interest. Reviewed results show that larvae were significantly affected by light characteristics. For example, European sea bass and sole larvae achieved the best performance, and showed fastest development and lowest degree of deformity under a light/dark cycle using blue light (half-peak bandwidth = 435–500 nm), conditions which were the closest to their natural aquatic environment. However, constant light (LL) or constant darkness (DD) was shown to negatively affect normal larval development and resulted in increased malformations and poor survival in most of the studied species. Similar results have been observed in other fish larvae such as Atlantic cod, which performed better under short wavelengths (blue and green). These findings highlight the role of lighting conditions during the early development of fish larvae and should be taken into account for the optimization of rearing protocols in fish hatcheries as juvenile supply is one of the main production bottlenecks.

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1. Introduction: development of biological clock and phototransduction system

Most living organisms inhabit a highly dynamic environment characterized by daily and annual photoperiod/light rhythms driven by the Earth's rotation on its axis and around the sun. Animals have adapted to these predictable changes by evolving a circadian system or biological clock to keep track of time, synchronize and anticipate periodic events such as sunrise/sunset and entrain rhythmic physiology and behaviour. To do so, animals develop photoreceptors and clock mechanisms during their early ontogeny according to a sequential set of events (Peirson et al., 2009). In fish, the development of an endogenous timing mechanism occurs very early, in zebrafish larvae, circadian rhythms of locomotor activity are found as soon as 5 days post-hatch (DPH) corresponding with the onset of active swimming behaviour and foraging activity (Vallone et al., 2007; Hurd and Cahill, 2002).

In teleost fish, light influences the entire life cycle from embryo development (Downing and Litvak, 2001) to sexual maturation in adults (Migaud et al., 2010). Although vision seems to be the primary sense involved in foraging activity and feeding (Puvanendran and

Brown, 2002), non-retinal photoreceptors, such as the pineal organ and deep brain photoreceptors, play key roles during larval development. The mechanisms by which these light sensitive structures mediate photoperiodic signals and entrain key physiological events are still not well understood in fish. Light stimuli perceived by the pineal are transduced via neural signals or as a hormonal signal through the rhythmic secretion of the time-keeping hormone melatonin (Amano et al., 2003; Falcon et al., 2010; Migaud et al., 2010). The biosynthesis and release of melatonin into the bloodstream is higher during the night or dark phase due to the photo-inhibition of the AA-NAT (arylalkylamine N-acetyltransferase) enzyme. Most interestingly, in fish larvae the pineal photoreceptors become functional and responsive to light before retinal photopigments. Most work in this field has been performed on the model species zebrafish where it has been shown that the molecular clock is functional and light reactive in the first day post fertilisation (Dekens and Whitmore, 2008), furthermore, the key enzyme controlling melatonin production, AA-NAT, is expressed at the blastula stage from the first day post-fertilisation which leads to initial melatonin synthesis occurring two nights after fertilisation (Gothilf et al., 1999; Kazimi and Cahill, 1999) all of which occurs prior to the development of the retinal pigments at 3 days post fertilisation (Gothilf et al., 1999).

In Atlantic halibut (*Hippoglossus hippoglossus*) lighting conditions can be tuned in order to synchronize the hatching time of embryos, as reported by Helvik and Bernt (1993), who found that exposure to light

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inhibited hatching, while returning to dark conditions before 18 DPF, resulted in synchronized hatching of all embryos within 90–140 min.

Survival of fish larvae may vary widely depending on the species and rearing conditions. For instance, sea bass survival rates were found to be higher in post-larvae reared at densities of 5 and 10 fish l^{-1} , than those reared at 15 and 20 fish l^{-1} (Hatzithanasiou et al., 2002) whereas Senegal sole survival was higher (81%) when larvae was exposed to a 10D:14L photoperiod regime (Cañavate et al., 2006). In other species like Atlantic cod, larvae showed low survival rates when reared under a light intensity of 2400 lx in a 0D:24L photoperiod (Puvanendran and Brown, 2002). Such variability in survival could be associated with a number of factors including lighting conditions.

Light is a complex environmental factor that depends on the lighting systems used (intensity and spectrum), the photoperiod, water absorbance properties as well as the specific light sensitivities of the species being reared. The aim of this paper is therefore to review a series of studies on the effects of artificial lighting conditions on the development of fish larvae, focusing in some species of European aquaculture interest.

2. Underwater photo-environment and biological responses

The physiology and behavioural traits observed in most aquatic organisms are the results of long term adaptations to light and temperature changes aiming to optimise the species survival. These environmental signals are complex and can display large variability over short periods of time during both daily and annual cycles. The main source of this photic variability in the aquatic environment is due to the fact that incident light is quickly modified (absorbance and reflection) depending on the specific properties of the water. The radiant energy from the sun (Fig. 1A) is selectively absorbed and scattered by particles present in the water column which thus affect the magnitude (square of the electric field vector), polarisation (direction of oscillation of the electric field vector), wavelength (frequency of oscillation), direction and propagation of the light (Smith, 1974). The water column acts as a potent chromatic filter with wavelengths below violet ($\lambda < 390$ nm) and beyond red ($\lambda > 600$ nm) being quickly absorbed. Blue wavelengths ($\lambda \sim 450$ nm) however,

penetrate deeper in the underwater environment, reaching depths of up to 150 m in the clearest ocean waters (Lalli and Parsons, 1995). In coastal and continental water, particles in suspension and substances originated from the decay of organic matter affect water transparency and spectral absorbance shifting the perceived spectral profile (Fig. 1C, D). Importantly, artificial lights differ greatly from the sun's spectrum, particularly underwater, as most light bulbs provide red-rich wavelengths and few blue photons (Fig. 1B).

Fish living in different underwater photo-environments appear to have adapted their maximum photopigment sensitivity accordingly (Kusmic and Gualtieri, 2000). This would suggest that the biological response to light depends on the species-specific ecology: in deep sea fishes, photoreceptors have a maximised visual contrast in the blue band, while coastal fish species have maximum sensitivity in the green band (Lythgoe, 1979). However while fish retinas have been well characterized at the ultrastructure level, the sensitivity to light remains unclear in most fish species. Fish retinas contain rods and cones that should respond to the wavelength range of the species' particular environmental niche (Bowmaker, 1990; Partridge and Cummings, 1998). For example, recent studies in salmonids have reported the presence of ultraviolet (UV), blue, green and red cones and rods in newly hatched larvae (Cheng et al., 2006) which aligns with a reported increased sensitivity to blue wavelengths of post-smolt Atlantic salmon (Migaud et al., 2007). However care should be taken in making broad conclusions about any particular species photic sensitivity as during their life cycle, fish can undergo significant geographical migrations which generally involve adaptations to their new photic environment. This process includes changes such as the development of a duplex retina (composed by rods and cones) (Neave, 1984) and the switch of the visual system from a high visual acuity to a high visual sensitivity during transitions from pelagic (larvae) to demersal or benthic habitats (juvenile) (Boeuf and Le Bail, 1999). Therefore, when designing an artificial lighting system for a given fish species in culture, its particular ecology and developmental stage which will affect its sensitivity should be considered.

In a rearing tank, the incident light is highly directional having generally originated from only one to a few point sources. Furthermore, the shallow and often clear water body of a fish tank has little

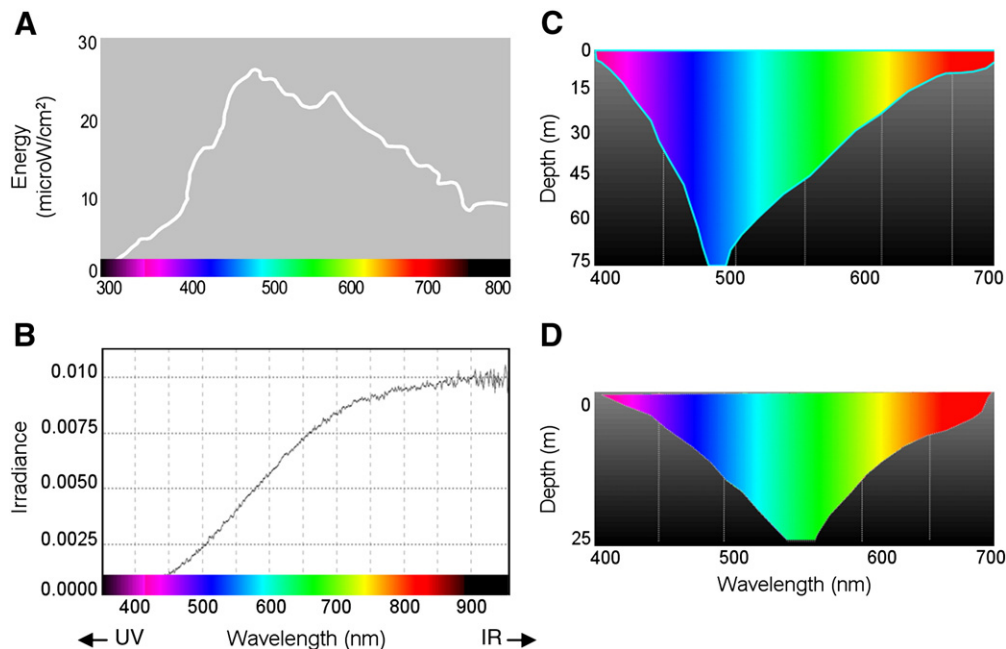


Fig. 1. Sunlight spectrum profile at the earth's surface (A) compared to the irradiance of an artificial light bulb (B). Typical underwater absorption of oceanic (C) and coastal or continental waters (D). Modified from Wolken (1995).

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